DEFOLIATION EFFECTS ON SPOTTED KNAPWEED SEED PRODUCTION AND VIABILITY

by

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ABSTRACT

Spotted knapweed (*Centaurea stoebe* L.) is a deeply taprooted perennial forb infesting millions of hectares of rangeland in western North America. Spotted knapweed forms large monocultures, which lowers plant diversity, reduces livestock and wildlife forage, and increases surface water runoff and sediment yield. It can produce 5,000-40,000 seeds · m^{-2} · $year^{-1}$, and often produces new flowers after prescribed sheep grazing or mowing defoliates spotted knapweed plants during the bolting or flowering stage. Research has yet to determine if new flowers produced following spring/summer defoliation produce viable seeds by the end of the growing season. The purpose of this 2-year study was to determine the appropriate timing(s) or combination(s) of timings of defoliation on spotted knapweed to reduce viable seed production. Ten spotted knapweed plants, located on spotted knapweed-infested rangeland in west-central Montana, were hand-clipped for each of the following treatments: 1) 35-40% relative utilization of above-ground biomass when plants were in the bolting stage; 2) 100% of buds removed at late-bud/early-flowering stage; 3) 100% of flowers removed at full-flowering stage; 4) Treatment 1+Treatment 2; 5) Treatment 1+Treatment 3; 6) Treatment 2+Treatment 3; 7) Treatment 1+Treatment 2+Treatment 3; and 8) unclipped control. The number of buds/flowerheads per plant, number of seeds per plant, percent viability of seeds, and number of viable seeds per plant were determined when seeds were in the well-developed stage, but seedhead bracts were still tightly closed (mid-August through September). Clipping at any timing or combination of timings reduced the number of buds/flowerheads per plant ($P < 0.01$), number of seeds per plant ($P < 0.01$), percent viability of seeds ($P < 0.01$), and number of viable seeds per plant ($P < 0.01$) both years compared with the unclipped control. Clipping during the bolting stage reduced the number of viable seeds by nearly 90% compared with no clipping. Clipping during the late-bud/early-flower or full-flower stage reduced the number of viable seeds by nearly 100% compared with no clipping. Defoliation of spotted knapweed via prescribed sheep grazing or mowing in summer should effectively suppress viable seed production of spotted knapweed.

CHAPTER 1

INTRODUCTION

Spotted knapweed (*Centaurea stoebe* L.) is an aggressive invader that may be the most significant threat to rangeland and pasture management in the Northern Intermountain Region (Harris and Cranston 1979; DiTomaso 2000). It is a perennial forb which was first recorded in North America in Victoria, British Columbia in 1893 (Watson and Renney 1974). Spotted knapweed currently infests every county in Washington, Idaho, Wyoming, and Montana (Sheley et al. 1998). It has spread at a rate of 27% per year in Montana with the potential to invade nearly half of all rangeland in the state (Lacey 1983; Carpinelli 2005). Spotted knapweed colonizes soils with a wide range of chemical and physical properties and is common in disturbed areas along roads, railroads, trails, and overgrazed rangelands (Watson and Renney 1974; Lacey et al. 1990). Although it is most common in disturbed areas (Watson and Renney 1974; Lacey et al. 1986; Lacey et al. 1990), spotted knapweed readily invaded pristine grasslands in Glacier National Park (Tyser and Key 1988). The ability of spotted knapweed to outcompete neighboring plants for water and nutrients allows it to form dense monocultures in areas once dominated by native bunchgrasses (Tyser and Key 1988; Olson 1999a). Spotted knapweed reduces livestock and wildlife forage (Watson and Renney 1974; Harris and Cranston 1979; Thompson 1996), lowers plant diversity (Tyser and Key 1988), and increases surface water runoff and sediment yield (Lacey et al. 1989). It is an economically destructive exotic species, causing over $42 million in losses annually to Montana's economy in direct and indirect costs (Hirsch and Leitch 1996).

High seed output and seed longevity make long-term control of spotted knapweed difficult and expensive (Schirman 1981; Griffith and Lacey 1991; Davis et al. 1993). Spotted knapweed reproduces by seed, with annual seed production ranging from 5,000 to 40,000 seeds $\cdot$ m^{-2} (Sheley et al. 1998), and current years' seeds average 60-82% viability (Jacobs and Sheley 1998). Spotted knapweed seed longevity also benefits its success. Seeds can remain viable in the soil for at least eight years (Davis et al. 1993).

Prescribed sheep grazing is a useful method of spotted knapweed control, especially when mechanical, cultural, biological, and chemical methods are restricted or constrained by environmental or economic concerns (Olson and Lacey 1994). Sheep can effectively be used to control spotted knapweed because sheep usually select broad-leaved forbs over grasses (Hanley 1982), sheep are adapted to grazing diverse topography (Olson and Lacey 1994), and sheep have a cleft upper lip and narrow muzzle which allows greater selectivity of plant parts (Arnold and Dudzinski 1978). Sheep readily graze spotted knapweed (Cox 1989; Launchbaugh and Hendrickson 2001; Thrift et al. 2008) and their use of this noxious weed may help re-establish a competitive balance between native grasses and spotted knapweed (Olson and Wallander 2001). Including sheep in a ranch operation not only provides weed control, but added income and enterprise diversification with wool and meat production. Preventing reproduction and the development of a seedbank is a key element when controlling a noxious weed (DiTomaso 2000). Chemical control of spotted knapweed is hampered by reinfestation from seed reserves in the soil (Nolan and Upadhyaya 1988). Sheep remove flowerheads of spotted knapweed (Olson and Wallander 2001), and sheep grazing of seedheads may effectively reduce seed production (Olson et al. 1997).

Fewer spotted knapweed seedheads are produced when plants are defoliated during the flowering stage than in the rosette or bolting stages (Launchbaugh and Hendrickson 2001). However, after defoliation occurs during the bolting or flowering stages, spotted knapweed often produces new, additional flowers before the end of the growing season (Watson and Renney 1974; Cox 1989). It has not been determined if the new flowers produced following defoliation contain viable seeds. Determining the timing of defoliation to best reduce viable seed production can improve the efficacy of prescribed sheep grazing or mowing for spotted knapweed control. The objective of this research was to determine the appropriate timing(s) or combination(s) of timings of defoliation on spotted knapweed to reduce viable seed production.

CHAPTER 2

LITERATURE REVIEW

History and Distribution of Spotted Knapweed

Spotted knapweed (*Centaurea stoebe* L.) is an invasive perennial forb that was first recorded in North America in Victoria, British Columbia in 1893 (Watson and Renney 1974). Spotted knapweed is native to grassland steppes of southeastern Europe and Asia Minor (Sheley et al. 1998). It was introduced into North America as a contaminant in alfalfa seed (*Medicago sativa* L.) and in discarded soil that was used as ship ballast (Duncan et al. 2001). Spotted knapweed currently infests every state except Alaska, Texas, Oklahoma, and Mississippi (USDA 2007), and is present in every county in Washington, Idaho, Wyoming, and Montana (Sheley et al. 1998). Spotted knapweed was first recorded in Montana in Ravalli County in 1920 and has since infested 1.5 million hectares in the state (MWSSC 2005). Since 1920, spotted knapweed has spread at a rate of 27% per year in Montana with the potential to invade half of all rangeland in the state (Lacey 1983; Carpinelli 2005).

Spotted Knapweed Biology and Ecology

Spotted knapweed belongs to the Asteraceae family and is morphologically distinguished by its alternate, divided leaves, black-tipped seedhead bracts, and purple flowers (Watson and Renney 1974). It is a deeply taprooted, rosette-forming perennial plant that can live up to nine years (Boggs and Story 1987; Sheley et al. 1998). The extensive taproot system allows it to extract moisture and nutrients from depths greater than most of the shallower fibrous roots common to the native perennial grasses it displaces (Weaver 1958; DiTomaso et al. 2003).

Spotted knapweed reproduces by seed (Story et al. 2001) and vegetatively when lateral shoots arise below the soil surface and horizontally grow for about 3 cm before forming a rosette that matures the following season, but does not detach from the parent root stock (Watson and Renney 1974). Spotted knapweed commonly produces 29 flowerheads $\cdot$ plant^{-1} and 32 seeds $\cdot$ flowerhead^{-1}, which is approximately 1,000 seeds $\cdot$ plant^{-1} annually (Story 1976). Annual seed production ranges from 5,000 to 40,000 seeds $\cdot$ meter^{-2} (Sheley et al. 1998), with current years' seeds averaging 60-82% viability (Jacobs and Sheley 1998). The number of seeds produced is largely affected by precipitation during the growing season, with greater seed production during wet years (Schirman 1981; Sheley et al. 1998). Spotted knapweed seed longevity also benefits the success of this noxious weed. Over 50% of buried seeds remain viable after five years and more than 25% are viable after eight years (Davis et al. 1993).

Spotted knapweed seeds germinate over a wide range of environmental conditions, germinate early, and grow rapidly (Sheley et al. 1993; Sheley et al. 1999). Spotted knapweed displays polymorphic germination, in which seeds on individual plants have different types of germination (Nolan and Upadhyaya 1988; Davis 1990). Nolan and Upadhyaya (1988) reported three types of germination in spotted knapweed: nondormant seeds germinated in darkness, light-sensitive dormant seeds germinated in response to red light, and light-insensitive dormant seeds failed to germinate after five days of continuous red light. Polymorphic germination, as well as asynchronous flowering behavior (not all flowerheads flower at the same time) of spotted knapweed, insures long-term survival of at least a portion of each seed crop (Davis 1990). Plants, such as spotted knapweed, that flower asynchronously are more likely to germinate polymorphically because environmental conditions vary when seeds develop (Fenner 1985; Davis 1990). In the absence of natural enemies, both herbivores and diseases, spotted knapweed plant growth and seed production are largely unrestricted, contributing to its success in North America (Locken and Kelsey 1987; Lacey et al. 1990).

Spotted knapweed buds form in early June, plants flower from July through September, and mature seeds are formed by mid-August (Watson and Renney 1974). Flowers bloom for 2-6 days, then close while the seeds mature (Chicoine 1984). Seeds are dispersed when the seedhead bracts dehydrate, and consequently open the seedhead 2-3 weeks after seed maturity. When plants are moved abruptly, seeds can scatter up to 1 meter from the plant (Strang et al. 1979), facilitating expansion of spotted knapweed infestations (Watson and Renney 1974). Spotted knapweed seeds can be transported by humans and animals. Flowerheads are transported to new locations when they attach to vehicle undercarriages, as well as shoes and clothing (Sheley et al. 1999). Animals disperse seeds that are caught in their coats or that have been ingested. Twenty-two percent of seeds remain viable after passing through the digestive system of a sheep (Wallander et al. 1995).

Spotted knapweed roots exude racemic (±)-catechin which acts as an allelochemical and an autoinhibitor (Bais et al. 2003; Weir et al. 2003; Veluri et al. 2004; Perry et al. 2005). Its allelochemical properties facilitate spotted knapweed invasion by inhibiting other species, while autoinhibition reduces intraspecific competition. (-)-Catechin is phytotoxic, inhibiting germination and stimulating cell death in the roots of other plant species, while (+)-catechin has antimicrobial and antifungal properties (Bais et al. 2003; Weir et al. 2003; Veluri et al. 2004; Weir et al. 2004). The combination of (-)-catechin and (+)-catechin likely facilitates spotted knapweed invasion. With the production of (±)-catechin, adult spotted knapweed plants inhibit spotted knapweed seedling root growth or germination, reducing intraspecific competition for the same resources. For example, in laboratory experiments (±)-catechin reduced spotted knapweed seedling root elongation by >50% (Perry et al. 2005) and (-)-catechin reduced the germination of spotted knapweed seeds (Weir et al. 2004). Within 2 weeks of germination, spotted knapweed seedlings begin to exude (±)-catechin, further reducing intraspecific competition by inhibiting establishment of siblings or neighboring plants (Weir et al. 2003). In response to the chemical signal from adults, spotted knapweed seeds postpone germination and avoid establishing in areas with high intraspecific competition which could prevent their survival (Perry et al. 2005). Because dormant spotted knapweed seeds can survive in the soil for at least eight years (Davis et al. 1993), seeds prevented from germinating by high soil (±)-catechin may outlive and eventually replace established spotted knapweed adults (Boggs and Story 1987).

The epidermal surface of spotted knapweed has glandular trichomes containing the sesquiterpene lactone cnicin (Locken and Kelsey 1987). Cnicin is allelopathic under suitable environmental and biotic conditions, which increases the competitiveness of spotted knapweed (Kelsey and Locken 1987). At higher concentrations, Kelsey and Locken (1987) reported that cnicin inhibited the germination of some plants including bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Love) and rough fescue (*Festuca campestris* Rydb.) and significantly inhibited seedling growth, especially root growth, in all species tested. The principle of allelopathy is not universally accepted and instead, physical factors in the habitat, availability of nutrients, and resource competition may be more important than allelopathy in determining the success of a species (Rizvi et al. 1992).

Spotted knapweed leaf tissues contain the highest concentration of cnicin, with low quantities in the inflorescence branches, stems, and seedheads (Locken and Kelsey 1987). Because cnicin is not leached from the roots, it is most likely released through the decomposition of litter, which is relatively slow and variable with spotted knapweed (Kelsey and Bedunah 1989; Davis 1990). Cnicin is bitter tasting to livestock (Olson and Kelsey 1997) and may deter herbivores from grazing spotted knapweed. Wildlife use of spotted knapweed may be limited by the low digestibility of knapweed stems and metabolic costs related to secondary compounds in stem leaves (Olson and Kelsey 1997; Wright and Kelsey 1997). However, studies report that herbivores such as sheep (Wallander et al. 1995; Olson and Wallander 2001; Sheley at al. 2004; Thrift et al. 2008), elk (*Cervus elaphus*), white-tailed deer (*Odocoileus virginianus*), and mule deer (*Odocoileus hemionus*) consume spotted knapweed (Wright and Kelsey 1997).

Environmental and Economic Impacts of Spotted Knapweed

Spotted knapweed colonizes soils with a wide range of chemical and physical properties and is common in disturbed areas along roads, railroads, and trails, on overgrazed rangeland (Watson and Renney 1974; Lacey et al. 1990), and in undisturbed areas (Tyser and Key 1988). Spotted knapweed readily invaded pristine grasslands in Glacier National Park (Tyser and Key 1988). This was facilitated by the roadside population of spotted knapweed and subsequent dispersal by animals and the creation of microhabitats by burrowing mammals, as well as natural expansion from colony borders. The ability of spotted knapweed to outcompete neighboring plants for water and nutrients allows it to form dense monocultures in areas once dominated by native bunchgrasses (Tyser and Key 1988; Olson 1999a). Native species richness and diversity are inversely related to spotted knapweed cover and biomass (Tyser and Key 1988; Kedzie-Webb et al. 2001). The dense overstory of spotted knapweed reduces the availability of more desirable forage species and reduces forage production (Watson and Renney 1974). Consequently, wildlife and livestock forage is reduced (Watson and Renney 1974; Harris and Cranston 1979; Thompson 1996).

Grasses minimize erosion by dissipating raindrops, covering soil, trapping soil particles, and increasing water infiltration and soil-holding capacity with fibrous roots (Olson 1999a). Erosion is more prevalent with the increase in bare ground, reduction in litter, and taproot associated with spotted knapweed (Lacey et al. 1989; Olson 1999a). Compared with a bunchgrass vegetation type, runoff and sediment yield were 56% and 192% greater, respectively, for a spotted knapweed-dominated site (Lacey et al. 1989). Lutgen and Rillig (2004) reported lower concentrations of glomalin, a glycoprotein produced by arbuscular mycorrhizal fungi (AMF), and shorter AMF hyphal lengths in areas with high spotted knapweed density on an upland range site in western Montana. Both of these factors correlate to soil structure and soil aggregate water stability. This study indicates that spotted knapweed may have a negative impact on soil quality in soils with lower aggregate stability, and soil structure can deteriorate in areas where spotted knapweed is not controlled.

Hirsch and Leitch (1996) estimated that the knapweed infestation of over 809,371 hectares in Montana has a direct negative impact of over $14 million annually. The total direct and secondary impacts total over $42 million annually, which could support over 500 full-time jobs in Montana.

Methods of Spotted Knapweed Control

Methods used to control spotted knapweed include herbicides, biological control agents, mowing, and prescribed grazing. Lacey et al. (1986) reported that picloram (Tordon), 2,4-D and dicamba are the most commonly used herbicides for spotted knapweed control. When applied at appropriate rates, these herbicides do not harm grasses and are selective for broad-leaved species. Therefore, these herbicides have the potential to damage other broad-leaved plants, including trees and shrubs. Picloram is the most effective herbicide for spotted knapweed control. Davis (1990) reported that picloram applied at 0.28 kg a.i. $\cdot$ ha^{-1} achieved 100% control of spotted knapweed for three years, depending on site conditions. Six years after the picloram treatments, mature spotted knapweed density within picloram treated plots was not significantly different than untreated control plots. Dicamba and 2,4-D treatments need to be applied annually until no viable seeds remain in the soil for effective control (Lacey et al. 1986), and picloram needs to be reapplied every three to five years because dormant seeds will still germinate once the herbicide residual dissipates. Excluding labor and equipment costs, ground application of herbicides costs a minimum of $61.75 per hectare (MWSSC 2005). With the need for frequent reapplication to deplete the seedbank (Sheley et al. 1999), herbicidal control of spotted knapweed is very expensive, especially for landowners with large acreages. Various environmental concerns may also surround the use of herbicides. The potential for water contamination, reduction in plant diversity when native broad-leaved species are sprayed, and human health concerns may all be issues associated with herbicide use.

Biological control agents that damage roots, shoots, leaves, or flowers, are used for spotted knapweed control (Sheley et al. 1999). *Urophora quadrifasciata* is a knapweed seedhead fly that deposits eggs inside the flower bud in early June (Lacey et al. 1986). Throughout the summer, larvae feed inside the flowerhead, causing the plant to devote its energy to forming a gall around the larvae rather than forming seeds. The seedhead flies *Urophora affinis* and *U. quadrifasciata* reduced the total number of seeds by 36% the first year and 41% the second year after introduction on a site in western Montana (Story et al. 1989). *Metzneria paucipunctella*, a small moth, feeds on knapweed florets and seeds. Two root-mining moths, *Agapeta zoegana* and *Pelochrista medullana*, produce larvae that girdle the roots and potentially kill the plants (Lacey et al. 1986). The root weevil (*Cyphocleonus achates*) larvae feed on the center of spotted knapweed roots (Jacobs et al. 2000). The root moths and root weevil are reducing spotted knapweed biomass production in several locations in Montana (Duncan et al. 2001). While the seed reduction caused by biological controls is important, it may not be a sufficient control method on its own, especially for spotted knapweed, which produces a large number of seeds each year (Myers and Risley 2000).

Season of mowing is more important than frequency of mowing, and a single annual mowing during the flowering or seed set stage for partial control of spotted knapweed is recommended (Rinella et al. 2001). This study, located on an Idaho fescue

(*Festuca idahoensis* Elmer)-bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Love) habitat type near Bozeman, Montana, also indicated that spotted knapweed was reduced more severely and consistently than grasses, which could lead to an increase in grasses and reduction in spotted knapweed over multiple years of mowing. Mowing during the flowering stage or bud and flowering stage significantly reduced the number of plants that produced seed and percent germination (Watson and Renney 1974), however, secondary flowering below the cutting height was observed. Mowing at the flowering stage or bud and flowering stage reduced seed germination from 91% to 19%. Mowing at the bud stage, flowering stage, or the bud and flowering stage reduced the number of seed-producing plants by 91%.

Revegetation may be important to manage spotted knapweed in areas where desirable plant species are absent and unable to occupy niches opened by weed control methods (Sheley et al. 1996). In these areas, successful management of spotted knapweed-infested rangeland and restoration of desired plant communities highly depends on the introduction and establishment of competitive plants (Sheley et al. 1996; Sheley et al. 2001). However, revegetation is not commonly used for spotted knapweed management due to the high cost and risk of failure (Jacobs et al. 1999; Sheley et al. 1999; Sheley et al. 2001). Revegetation becomes expensive on spotted knapweed-infested rangeland because multiple attempts and entries onto a site are typically required to maximize desired species seedling establishment (Jacobs et al. 1999; Sheley et al. 2001). Usually revegetation involves late-fall disking of the site and applying herbicide to reduce the weed seedbank, then fall dormant grasses are seeded (Jacobs et al. 1999;

Sheley et al. 2001). If the grass seedlings survive into mid-summer the following year, herbicide is applied at a reduced rate or mowing is used to reduce weed competition.

Prescribed Sheep Grazing for Spotted Knapweed Control

Sheep grazing is a useful method of spotted knapweed control, especially when mechanical, cultural, biological, and chemical methods are restricted or constrained by environmental or economic concerns (Olson and Lacey 1994). Unlike cattle (*Bos taurus*), which usually consume more grass and fibrous forage, sheep (*Ovis aries*) are intermediate feeders that actively select for a greater number of forbs in their diet (Hanley 1982; Olson 1999b; Olson and Wallander 2001), making them an ideal species for broad-leaf weed control. Sheep are successful on poor quality rangeland, and their small body size, ruminant digestive system, and small mouth size enable greater selectivity and reduce time-energy constraints on foraging (Arnold 1962; Hanley 1982). Sheep have a muscular pad in their upper jaw, a cleft upper lip, and a narrow muzzle which allows greater selectivity of plant parts (Arnold and Dudzinski 1978). Sheep are adapted to grazing steep topography, enabling them to graze weeds in areas that are inaccessible to other weed control methods (Olson and Lacey 1994). While it costs approximately $61.75 per hectare to apply herbicides (MWSSC 2005), it is estimated to cost $9.41 per hectare to use sheep as a weed control method (Montana Sheep Institute, unpublished data).

Sheep readily graze spotted knapweed (Cox 1989; Launchbaugh and Hendrickson 2001; Thrift et al. 2008) and their use of this noxious weed may help re-establish a competitive balance between native grasses and spotted knapweed (Olson and Wallander

2001). In a light spotted knapweed infestation (13% of vegetative composition) on foothill rangeland in western Montana, sheep diets averaged 26% spotted knapweed and averaged 64% in a moderate spotted knapweed infestation (36% of vegetative composition), while relative utilization of graminoids was light in both infestations (15% in June and 31% in July) (Thrift et al. 2008). Because spotted knapweed is negatively impacted by repeated sheep grazing, while the native grass community is minorly impacted when grazing is properly implemented, spotted knapweed is a hopeful candidate for control by prescription grazing (Olson et al. 1997; Launchbaugh and Hendrickson 2001). Olson and Wallander (2001) documented that the sheep in their study removed flowerheads and leaves of spotted knapweed. Lacey et al. (1986) noted that flower buds and seedheads are often grazed in late summer. Spotted knapweed flowerheads contain only trace amounts of cnicin (Kelsey and Mihalovich 1987; Locken and Kelsey 1987). Although cnicin in spotted knapweed is bitter tasting to livestock (Olson and Kelsey 1997), sheep eagerly eat bitter and acrid tasting weeds (Olson and Lacey 1994). When diet composition of spotted knapweed exceeds 70%, cnicin has anti-microbial properties that depress sheep rumen microbial activity and mass in vitro (Olson and Kelsey 1997). Sheep diets are diverse to counteract the toxic effects of secondary compounds (Olson and Wallander 2001).

Including sheep in a ranch operation not only provides weed control, but also added income and enterprise diversification with wool and meat production. Spotted knapweed can also be nutritious forage. In western Montana, Kelsey and Mihalovich (1987) reported that the nutrient content of spotted knapweed in the spring was comparable to native forage plants and was adequate to meet livestock needs, and these authors encouraged grazing of spotted knapweed to reduce forage loss and reduce knapweed size and seed production. The nutritive values of spotted knapweed leaves and flowerheads was higher than that of Idaho fescue on a site near Bozeman, Montana at 1,570 m elevation (Olson and Wallander 2001). On foothill rangeland in western Montana, nutritive quality of sheep diets grazing spotted knapweed infested rangeland in June and July was similar to sheep grazing uninfested rangeland (Thrift et al. 2008).

Spotted knapweed water and nutrient uptake and carbohydrate allocation may be affected by necrosis of grazed spotted knapweed crowns, reducing the plant's competitive ability and shortening its life span (Olson et al. 1997). A greenhouse clipping study found that monthly defoliations of spotted knapweed at 50% relative utilization during the growing season reduced carbohydrate concentrations in stems, crowns, and roots (Lacey et al. 1994). Another greenhouse clipping study reported that a single clipping of 75% relative utilization during the bolting stage reduced vigor and standing crop of spotted knapweed, but a single clipping at 25% relative utilization during the bolting stage did not have the same effect (Kennett et al. 1992). These studies also found that defoliations at monthly intervals were more effective than a single defoliation at reducing spotted knapweed root and crown weights, and carbohydrate concentrations.

In a field experiment, clipping 50% of spotted knapweed aboveground biomass in early summer and again in late summer reduced final biomass by 40% at the end of the season (Newingham and Callaway 2006). However, total biomass production and reproductive output were not affected by this clipping. In a moderate spotted knapweed infestation (36% of vegetative composition), spotted knapweed utilization was greater and graminoid utilization less when sheep grazed in July rather than June (Thrift et al.

2008). This study also found that in a light spotted knapweed infestation (13% of vegetative composition), relative utilization of graminoids was less and spotted knapweed utilization greater when sheep grazed in June rather than July. In southeastern Idaho, defoliating spotted knapweed, either alone or in combination with associated vegetation, greatly reduced spotted knapweed seedhead production and fewer spotted knapweed seedheads were produced when plants were defoliated in the flowering stage than in the bolting or rosette stages (Launchbaugh and Hendrickson 2001) .

Implementing prescribed sheep grazing and other control methods in an integrated weed management plan can lead to successful management of undesirable plants (Brock 1988; Lacey et al. 1994; Popay and Field 1996). Removing adult spotted knapweed plants with a spring 2,4-D application combined with repeated sheep grazing to control seedling and juvenile plants reduced spotted knapweed density, cover, and biomass, which allowed residual grasses to reoccupy the site (Sheley et al. 2004). An integrated weed management plan that combines grazing, herbicides, and biological control agents can most effectively suppress spotted knapweed (Jacobs et al. 1999; Sheley et al. 1999).

Preventing reproduction and development of a seedbank is a key element to suppressing a noxious weed (DiTomaso 2000). High seed output and seed longevity make long-term control of spotted knapweed difficult and expensive (Schirman 1981; Griffith and Lacey 1991; Davis et al. 1993). Chemical control is hampered by reinfestation from seed reserves in the soil (Nolan and Upadhyaya 1988). Because sheep selectively remove spotted knapweed seedheads when grazing (Lacey et al. 1986; Olson and Wallander 2001), prescribed sheep grazing could be used as an effective tool to reduce seed production and consequent contribution to the seedbank. The formula for creating a prescribed grazing plan includes type of grazing animal, timing, duration, and intensity (Frost and Launchbaugh 2003). Previous research indicates how defoliation affects spotted knapweed biomass and surrounding vegetation, but how timing of defoliation affects spotted knapweed seed production and viability has yet to be determined. Understanding the optimal time of defoliation to reduce spotted knapweed seed production and viability is a key component of a grazing prescription to suppress this noxious weed species.

Literature Cited

Arnold, G. W. 1962. Effects of pasture maturity on the diet of sheep. *Australian Journal of Agricultural Research* 13:701-706.

Arnold, G. W., and M. L. Dudzinski. 1978. Ethology of free ranging domestic animals. New York, NY: Elsevier Scientific Publishing. 198 p.

Bais, H. P., R. Vepachedu, S. Gilroy, R. M. Callaway, and J. M. Vivanco. 2003. Allelopathy and exotic plant invasion: from molecules and genes to species interactions. *Science* 301:1377-1380.

Boggs, K. W., and J. M. Story. 1987. The population age structure of spotted knapweed (*Centaurea maculosa*) in Montana. *Weed Science* 35:194-198.

Brock, J. H. 1988. Livestock: biological control in brush/weed management programs. *Rangelands* 10:32-34.

Carpinelli, M. 2005. *Plant conservation alliance's alien plant working group. Available at:* http://www.nps.gov/plants/alien/. *Accessed 6 October 2007.*

Chicoine, T. K. 1984. Spotted knapweed (*Centaurea maculosa* L.) control, seed longevity, and migration in Montana [thesis]. Bozeman, MT: Montana State University. 83 p.

Cox, J. W. 1989. Observations, experiments and suggestions for research on the sheep-spotted knapweed relationship. *In*: P. K. Fay and J. R. Lacey [EDS.], Proceedings of the Knapweed Symposium. 4-5 April 1989; Bozeman, MT: Montana State University, Plant and Soil Science Department. p. 79-82.

Davis, E. S. 1990. Spotted knapweed (*Centaurea maculosa* L.) seed longevity, chemical control and seed morphology [thesis]. Bozeman, MT: Montana State University. 109 p.

Davis, E. S., P. K. Fay, T. K. Chicoine, and C. A. Lacey. 1993. Persistence of spotted knapweed (*Centaurea maculosa*) seed in soil. *Weed Science* 41:57-61.

DiTomaso, J. M. 2000. Invasive weeds in rangelands: species, impacts, and management. *Weed Science* 48:255-265.

DiTomaso, J. M., G. B. Kyser, and C. B. Pirosko. 2003. Effect of light and density on yellow starthistle (*Centaurea solstitialis*) root growth and soil moisture use. *Weed Science* 51:334-341.

Duncan, C., J. Story, and R. Sheley. 2001. *Montana knapweeds: identification, biology, and management. Available at:* http://www.montana.edu/wwwpb/pubs/knapweed/circ311.html. *Accessed 1 November 2007.*

Fenner, M. 1985. Seed ecology. New York, NY: Chapman and Hall. 151 p.

Frost, R. A., and K. L. Launchbaugh. 2003. Prescription grazing for rangeland weed management. *Rangelands* 25:43-47.

Griffith, D., and J. R. Lacey. 1991. Economic evaluation of spotted knapweed (*Centaurea maculosa*) control using picloram. *Journal of Range Management* 44:43-47.

Hanley, T. A. 1982. The nutritional basis for food selection by ungulates. *Journal of Range Management* 35:146-151.

Harris, P., and R. Cranston. 1979. An economic evaluation of control methods for diffuse and spotted knapweed in western Canada. *Canadian Journal of Plant Science* 59:375-382.

Hirsch, S. A., and J. A. Leitch. 1996. The impact of knapweed on Montana's economy. Fargo, ND: North Dakota State University Agricultural Experiment Station, Agricultural Economics Report 355. 43 p.

Jacobs, J. S., and R. L. Sheley. 1998. Observation: life history of spotted knapweed. *Journal of Range Management* 51:665-673.

Jacobs, J. S., M. F. Carpinelli, and R. L. Sheley. 1999. Revegetating noxious weed-infested rangeland. *In*: R. L. Sheley and J. K. Petroff [EDS.]. Biology and management of noxious rangeland weeds. Corvallis, OR: Oregon State University Press. p. 133-141.

Jacobs, J. S., R. L. Sheley, and J. M. Story. 2000. Use of picloram to enhance establishment of *Cyphocleonus achates* (Coleoptera: Curculionidae). *Environmental Entomology* 29:349-354.

Kedzie-Webb, S. A., R. L. Sheley, J. J. Borkowski, and J. S. Jacobs. 2001. Relationships between *Centaurea maculosa* and indigenous plant assemblages. *Western North American Naturalist* 61:43-49.

Kelsey, R. G., and D. J. Bedunah. 1989. Ecological significance of allelopathy for *Centaurea* species in the northwestern United States. *In*: P. K. Fay and J. K. Lacey [EDS.], Proceedings of the Knapweed Symposium. 4-5 April 1989; Bozeman, MT: Montana State University. p. 10-32.

Kelsey, R. G., and L. J. Locken. 1987. Phytotoxic properties of cnicin, a sesquiterpene lactone from *Centaurea maculosa* (spotted knapweed). *Journal of Chemical Ecology* 13: 19-33.

Kelsey, R. G., and R. D. Mihalovich. 1987. Nutrient composition of spotted knapweed (*Centaurea maculosa*). *Journal of Range Management* 40:277-281.

Kennett, G. A., J. R. Lacey, C. A. Butt, K. M. Olson-Rutz, and M. R. Haferkamp. 1992. Effects of defoliation, shading and competition on spotted knapweed and bluebunch wheatgrass. *Journal of Range Management* 45:363-369.

Lacey, C. A., J. R. Lacey, T. K. Chicoine, P. K. Fay, and R. A. French. 1986. Controlling knapweed on Montana rangeland. Bozeman, MT: Montana State University Extension Service Circular 311. 15 p.

Lacey, J. R. 1983. A complete takeover by knapweed in 2001? *Montana Farmer-Stockman* 70:32-34.

Lacey, J. R., C. B. Marlow, and J. R. Lane. 1989. Influence of spotted knapweed (*Centaurea maculosa*) on surface runoff and sediment yield. *Weed Technology* 3:627-631.

Lacey, J., P. Husby, and G. Handl. 1990. Observations on spotted and diffuse knapweed invasion into ungrazed bunchgrass communities in western Montana. *Rangelands* 12:30-32.

Lacey, J. R., K. M. Olson-Rutz, M. R. Haferkamp, and G. A. Kennett. 1994. Effects of defoliation and competition on total non-structural carbohydrates of spotted knapweed. *Journal of Range Management* 47:481-484.

Launchbaugh, K., and J. Hendrickson. 2001. Prescription grazing for *Centaurea* control on rangelands. *In:* L. Smith [ED.]. The First International Knapweed Symposium of the Twenty-First Century. 15-16 March 2001; Coeur d' Alene, ID: USDA, Agricultural Research Service. p. 27-32.

Locken, L. J., and R. G. Kelsey. 1987. Cnicin concentrations in *Centaurea maculosa*, spotted knapweed. *Biochemical Systematics and Ecology* 15:313-320.

Lutgen, E. R., and M. C. Rillig. 2004. Influence of spotted knapweed (*Centaurea maculosa*) management treatments on arbuscular mycorrhizae and soil aggregation. *Weed Science* 52:172-177.

[MWSSC] Montana Weed Summit Steering Committee. 2005. The Montana weed management plan, revised. Helena, MT: Montana Department of Agriculture. 88 p.

Myers, J. H., and C. Risley. 2000. Why reduced seed production is not necessarily translated into successful biological weed control. *In*: N. R. Spencer [ED.], Proceedings of the X International Symposium on Biological Control of Weeds. 4-14 July 1999; Bozeman, MT: Montana State University. p. 569-581.

Newingham, B. A., and R. M. Callaway. 2006. Shoot herbivory on the invasive plant, *Centaurea maculosa*, does not reduce its competitive effects on conspecifics and natives. *Oikos* 114:397-406.

Nolan, D. G., and M. K. Upadhyaya. 1988. Primary seed dormancy in diffuse and spotted knapweed. *Canadian Journal of Plant Science* 68:775-783.

Olson, B. E. 1999a. Impacts of noxious weeds on ecologic and economic systems. *In*: R. L. Sheley and J. K. Petroff [EDS.]. Biology and management of noxious rangeland weeds. Corvallis, OR: Oregon State University Press. p. 4-18.

Olson, B. E. 1999b. Manipulating diet selection to control weeds. *In*: K. L. Launchbaugh, K. D. Sanders, and J. C. Mosley [EDS.]. Grazing behavior of livestock and wildlife. Moscow, ID: University of Idaho, Idaho Forest, Wildlife, and Range Experiment Station Bulletin #70. p. 36-44.

Olson, B. E., and R. G. Kelsey. 1997. Effect of *Centaurea maculosa* on sheep rumen microbial activity and mass. *Journal of Chemical Ecology* 23:1131-1144.

Olson, B. E., R. T. Wallander, and J. R. Lacey. 1997. Effects of sheep grazing on a spotted knapweed-infested Idaho fescue community. *Journal of Range Management* 50:386-390.

Olson, B. E., and J. R. Lacey. 1994. Sheep: a method for controlling rangeland weeds. *Sheep Research Journal* 10:105-112.

Olson, B. E., and R. T. Wallander. 2001. Sheep grazing spotted knapweed and Idaho fescue. *Journal of Range Management* 54:25-30.

Perry, L. G., G. C. Thelen, W. M. Ridenour, T. L. Weir, R. M. Callaway, M. W. Paschke, and J. M. Vivanco. 2005. Dual role for an allelochemical: (±)-catechin from *Centaurea maculosa* root exudates regulates conspecific seedling establishment. *Journal of Ecology* 93:1126-1135.

Popay, I., and R. Field. 1996. Grazing animals as weed control agents. *Weed Technology* 10:217-231.

Rinella, M. J., J. S. Jacobs, R. L. Sheley, and J. J. Borkowski. 2001. Spotted knapweed response to season and frequency of mowing. *Journal of Range Management* 54:52-56.

Rizvi, S. J. H., H. Haque, V. K. Singh, and V. Rizvi. 1992. A discipline called allelopathy. *In*: S. J. H. Rizvi and V. Rizvi [EDS.]. Allelopathy: basic and applied aspects. London: Chapman and Hall. p. 1-10.

Schirman, R. 1981. Seed production and spring seedling establishment of diffuse and spotted knapweed. *Journal of Range Management* 34:45-47.

Sheley, R. L., L. L. Larson, and D. E. Johnson. 1993. Germination and root dynamics of range weeds and forage species. *Weed Technology* 7:234-237.

Sheley, R. L., T. J. Svejcar, and B. D. Maxwell. 1996. A theoretical framework for developing successional weed management strategies on rangeland. *Weed Technology* 10:766-773.

Sheley, R. L., J. S. Jacobs, and M. F. Carpinelli. 1998. Distribution, biology, and management of diffuse (*Centaurea diffusa*) and spotted knapweed (*Centaurea maculosa*). *Weed Technology* 12:353-362.

Sheley, R. L., J. S. Jacobs, and M. L. Carpinelli. 1999. Spotted knapweed. *In*: R. L. Sheley and J. K. Petroff [EDS.]. Biology and management of noxious rangeland weeds. Corvallis, OR: Oregon State University Press. p. 350-361.

Sheley, R. L., J. S. Jacobs, and D. E. Lucas. 2001. Revegetating spotted knapweed infested rangeland in a single entry. *Journal of Range Management* 54:144-151.

Sheley, R. L., J. S. Jacobs, and J. M. Martin. 2004. Integrating 2,4-D and sheep grazing to rehabilitate spotted knapweed infestations. *Journal of Range Management* 57:371-375.

Story, J. M. 1976. A study of *Urophora affinis* (Diptera: Tephritidae) released on spotted knapweed in western Montana [thesis]. Bozeman, MT: Montana State University. 77 p.

Story, J. M., K. W. Boggs, and R. M. Nowierski. 1989. Effect of two introduced seed head flies on spotted knapweed. *Montana Agriculture Research* 6:14-17.

Story, J. M., L. Smith, and W. R. Good. 2001. Relationship among growth attributes of spotted knapweed (*Centaurea maculosa*) in western Montana. *Weed Technology* 15:750-761.

Strang, R. M., K. M. Lindsay, and R. S. Price. 1979. Knapweeds: British Columbia's undesirable aliens. *Rangelands* 1:141-143.

Thompson, M. J. 1996. Winter foraging response of elk to spotted knapweed removal. *Northwest Science* 70:10-19.

Thrift, B. D., J. C. Mosley, T. K. Brewer, B. C. Roeder, B. E. Olson, and R. W. Kott. 2008. Prescribed sheep grazing to suppress spotted knapweed on foothill rangeland. *Rangeland Ecology and Management* 61:18-25.

Tyser, R. W., and C. H. Key. 1988. Spotted knapweed in natural area fescue grasslands: an ecological assessment. *Northwest Science* 62:151-160.

USDA, NRCS. 2007. *The PLANTS database. Available at:* http://plants.usda.gov. *Accessed 6 October 2007.*

Veluri, R., T. L. Weir, H. P. Bais, F. R. Stermitz, and J. M. Vivanco. 2004. Phytotoxic and antimicrobial activities of catechin derivatives. *Journal of Agricultural and Food Chemistry* 52:1077-1082.

Wallander, R. T., B. E. Olson, and J. R. Lacey. 1995. Spotted knapweed seed viability after passing through sheep and mule deer. *Journal of Range Management* 48:145-149.

Watson, A. K., and A. J. Renney. 1974. The biology of Canadian weeds. *Centaurea diffusa* and *C. maculosa*. *Canadian Journal of Plant Science* 54:687-701.

Weaver, J. E. 1958. Classification of root systems of forbs of grassland and a consideration of their significance. *Ecology* 39:394-401.

Weir, T. L., H. P. Bais, and J. M. Vivanco. 2003. Intraspecific and interspecific interactions mediated by a phytotoxin, (-)-catechin, secreted by the roots of *Centaurea maculosa* (spotted knapweed). *Journal of Chemical Ecology* 29:2397-2412.

Weir, T. L., S. W. Park, and J. M. Vivanco. 2004. Biochemical and physiological mechanisms mediated by allelochemicals. *Current Opinion in Plant Biology* 7:472-479.

Wright, A. L., and R. G. Kelsey. 1997. Effects of spotted knapweed on a cervid winter-spring range in Idaho. *Journal of Range Management* 50:487-496.

CHAPTER 3

EFFECTS OF TIMING OF DEFOLIATION ON SPOTTED KNAPWEED SEED PRODUCTION AND VIABIITY

Introduction

Spotted knapweed (*Centaurea stoebe* L.) is a deeply taprooted perennial forb infesting millions of hectares of native rangeland in the United States (Jacobs and Sheley 1998). Spotted knapweed was first recorded in the Pacific Northwest in the late 1800s (Watson and Renney 1974). It currently infests every state except Alaska, Texas, Oklahoma, and Mississippi (USDA 2007a). Since first being recorded in Montana in 1920, this noxious weed has spread at a rate of 27% per year, with the potential to invade half of all rangeland in the state (Lacey 1983; Carpinelli 2005). Over $42 million is lost annually to Montana's economy in direct and indirect costs associated with spotted knapweed (Hirsch and Leitch 1996). Unlike other invasive species, spotted knapweed does not require disturbance to invade an area. It can readily establish itself on pristine rangelands (Tyser and Key 1988). Spotted knapweed is capable of forming large monocultures, lowers plant diversity (Tyser and Key 1988), reduces livestock and wildlife forage (Watson and Renney 1974; Harris and Cranston 1979; Thompson 1996), and increases surface water runoff and sediment yield (Lacey et al. 1989).

Spotted knapweed is a prolific seed producer, producing 5,000 to 40,000 seeds $\cdot$ m^{-2} each year (Sheley et al. 1998), with current years' seeds averaging 60-82% viability (Jacobs and Sheley 1998). Seeds can remain viable in the soil for at least eight years (Davis et al. 1993). Herbicides are commonly used for spotted knapweed control, however, chemical control is hampered by reinfestation from seed reserves in the soil (Nolan and Upadhyaya 1988). High seed output and seed longevity in the soil make long-term control of spotted knapweed difficult and expensive (Schirman 1981; Griffith and Lacey 1991; Davis et al. 1993). A key to suppressing a noxious weed is preventing reproduction and the development of a seedbank (DiTomaso 2000).

Sheep grazing is a useful method of spotted knapweed control, especially when mechanical, cultural, biological, and chemical methods are restricted or constrained by environmental or economic concerns (Olson and Lacey 1994). Using prescribed sheep grazing as a spotted knapweed control method may cause less harm to soils, water, plants, and other organisms than herbicides, and it also adds income and enterprise diversification with wool and meat production. Sheep can effectively be used to control spotted knapweed because this species usually prefers broad-leaved forbs over grasses (Hanley 1982), is adapted to grazing steep topography (Olson and Lacey 1994), and has a cleft upper lip and narrow muzzle, allowing greater selectivity of plant parts (Arnold and Dudzinski 1978). Sheep graze spotted knapweed buds and flowerheads, including in late summer (Lacey et al. 1986; Olson and Wallander 2001), and their use of seedheads can be utilized to reduce seed production (Olson et al. 1997). Sheep grazing this noxious weed may help re-establish a competitive balance between native grasses and spotted knapweed (Olson and Wallander 2001).

In western Montana, even when desirable forage was available, relative utilization of spotted knapweed by sheep averaged 35 to 50% in June or July, and relative utilization of graminoids averaged 15% except under exceptionally hot and dry conditions (Thrift et al. 2008). In southeastern Idaho, fewer spotted knapweed seedheads were produced when plants were defoliated in the flowering stage than in the bolting or rosette stages (Launchbaugh and Hendrickson 2001). Three summers of sheep grazing in southwestern Montana reduced the number of viable seeds in the seedbank by 54%, while the number of viable seeds in the soil of the ungrazed control site increased 88% during the 3-year period (Olson et al. 1997). Mowing during the flowering stage or bud and flowering stage reduced seed germination from 91% to 19%, and mowing during the bud stage, flowering stage, or the bud and flowering stage reduced the number of seed-producing plants by 91% (Watson and Renney 1974).

However, spotted knapweed produces new, additional flowers before the end of the growing season after being defoliated during the bolting or flowering stages (Watson and Renney 1974; Cox 1989). Research has yet to determine if these new flowers produce viable seed. Because spotted knapweed is a prolific seed producer, understanding the optimal timing(s) of defoliation to reduce viable seed production and consequent input into the seedbank would improve the efficacy of sheep grazing for spotted knapweed control. The objective of my research was to determine the appropriate timing(s) or combination(s) of timings of defoliation on spotted knapweed to reduce viable seed production.

Materials and Methods

Study Area

This 2-year study was located 5 km east of Helmville, Montana (46˚ 98' N, 113˚ 05' W). The ecological site is Silty, in the 380 to 480-mm Precipitation Zone (USDA 2007b). The elevation of the site is approximately 1400 m and it is classified as a rough fescue (*Festuca campestris* Rydb.)/bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Love) habitat type (Mueggler and Stewart 1980). The 30-year average annual precipitation is 318 mm, with 56% occurring as rain between May and September (WRCC 2007). The 30-year average minimum and maximum temperatures are 3.8 and 21.8°C in June, 5.3 and 26.6°C in July, 4.1 and 26.7°C in August, and -0.3 and 20.7°C in September, respectively. In addition to spotted knapweed, the dominant forb, other major forb species on the site include lupine (*Lupinus* L. spp.), western yarrow (*Achillea millefolium* L.), yellow salsify (*Tragopogon dubius* Scop.), common dandelion (*Taraxacum officinale* G. H. Weber ex Wiggers), and wild onion (*Allium* L. spp.). Idaho fescue (*Festuca idahoensis* Elmer), green needlegrass (*Nassella viridula* (Trin.) Barkworth), Sandberg bluegrass (*Poa secunda* J. Presl), and bluebunch wheatgrass are the predominant grass species. Mountain big sagebrush (*Artemisia tridentata* Nutt. ssp. *vaseyana* (Rydb.) Beetle) is the dominant shrub on the site.

Treatments

Eighty single-stem spotted knapweed plants between 23 and 36 cm in height were selected each year (2006, 2007) on a site moderately infested with spotted knapweed (36% of vegetative composition). The areas containing the 80 plants (286 m^2) were fenced with 1.8 m tall welded wire panels to exclude ungulate grazing. The 2007 exclosure was located about 75 meters from the 2006 exclosure to ensure that results from the two years were independent. Individual plants were located a minimum of one meter apart, and identification tags were placed at the base of each stem. Before the June treatment each year, to account for potential competition surrounding each treatment plant, percent canopy cover of spotted knapweed, lupine, and perennial graminoids was estimated inside a 1-meter diameter (0.79 m^2) hoop surrounding each plant and the initial height of each treatment plant was measured to the nearest centimeter. Eight hand-clipped treatments emulating observed sheep grazing behavior were applied to the individual spotted knapweed plants, with ten plants included in each of the eight treatments (n = 80 plants per year).

Treatments included: 1) clip plants to 9-cm stubble height (35-40% relative utilization) during bolting stage (mid-June); 2) remove 100% of buds/flowers+3 cm of foliage beneath buds during late-bud/early-flower stage (mid-July); 3) remove 100% of flowers+3 cm of foliage beneath buds during full flower stage (mid-August); 4) Treatment 1+Treatment 2 (June and July); 5) Treatment 1+Treatment 3 (June and August); 6) Treatment 2+Treatment 3 (July and August); 7) Treatment 1+Treatment 2+ Treatment 3 (June, July, and August); and 8) unclipped control. The 35-40% relative utilization used for Treatment 1 was determined by a previous study at the same study site, in which the relative utilization of spotted knapweed by sheep grazing on a landscape scale was 35-40% during the bolting stage (Thrift et al. 2008). The 3 cm of foliage clipped beneath the buds was based on personal observations of how sheep graze spotted knapweed buds and flowers and resulted in lighter relative utilization of spotted knapweed in July and August than in the June treatment. Overall, clipping in June, July, or August resulted in a light defoliation intensity on spotted knapweed plants.

Response Variables

Response variables in this study included: 1) number of buds/flowers per plant; 2) number of doughy, intermediate, and mature seeds per plant; 3) total number of seeds per plant; 4) percent viability of doughy, intermediate, and mature seeds; 5) number of viable doughy, intermediate, and mature seeds per plant; and 6) total number of viable seeds per plant. Buds and flowers were collected from treatment plants when at least 50% of the plants within a treatment were in the post-flowering stage, when seeds were well-developed but the bracts were still tightly closed, and before seed dispersal (Watson and Renney 1974), which occurred from mid-August through September.

<u>Number of Buds/Flowerheads</u> For each treatment, the number of buds and flowerheads per plant was counted prior to being collected. Immature buds, distinguished from newly forming leaves by visible bracts, were included in the final count. The number of buds/flowerheads with evidence of gall fly (*Urophora quadrifasciata* (Meigen)) damage was recorded during bud/flowerhead collection.

<u>Number of Seeds</u> The number of doughy, intermediate, and mature seeds per plant and total number of seeds per plant were counted in the laboratory. Seeds were extracted from seedheads using a rub board. Seeds from each plant were then divided into three developmental stages: 1) doughy (tiny, flat, seedcoat nearly translucent), 2) intermediate (medium-sized, somewhat filled, seedcoat light brown), and 3) mature (large, full and rounded, seedcoat hard and black) and were counted by stage. Total number of seeds per plant was calculated by adding the number of seeds in each of the three developmental stages. When seedheads were taken apart using a rub board, the number of seedheads with evidence of gall fly damage was recorded.

<u>Percent Viability of Seeds</u> Seeds were tested for viability using the tetrazolium (TZ) test (Grabe 1970). Three subsamples from each of the doughy, intermediate, and mature developmental stages of each treatment plant were used. Seeds within a given

developmental stage were randomly assigned to one of three subsamples. Each subsample contained either 20 seeds or one-third of the total number of seeds in that developmental stage, whichever was greater. Percent viability was calculated by averaging the proportion of viable seeds in each of the three subsamples.

Number of Viable Seeds The number of viable doughy, intermediate, and mature seeds per plant and the total number of viable seeds per plant were determined using values from the number of seeds per plant and the percent viability of seeds. The number of viable doughy, intermediate, and mature seeds was calculated by multiplying the number of seeds in each developmental stage by the percent viability of seeds in each respective developmental stage. Total viable seeds per plant were calculated by summing the number of viable seeds in the three developmental stages.

Statistical Analysis

The experimental design for this study was completely randomized. Treatments were arranged in an 8 x 2 factorial arrangement, with 8 timings/combinations of timings of defoliation and 2 years. Individual plants were the experimental units.

Data were analyzed using the GLM procedure of SAS (SAS 2004). Percent data and non-percent data that were not normally distributed were arcsine and square root transformed, respectively, to stabilize variances and better approximate normal distribution of residuals (Steel and Torrie 1980; Kuehl 2000). Means and standard errors presented in the text and tables are from untransformed data. Analysis of covariance (ANCOVA) was used to compare responses among treatments. Percent canopy cover of spotted knapweed, lupine, and perennial graminoids, the percent of buds/flowers with evidence of gall fly damage, and initial plant height were used as covariables in the analyses. Differences were considered significant at $P \leq 0.05$.

Results

Number of Buds/Flowerheads

Clipping in June or July (i.e., spotted knapweed plants in bolting stage or late-bud/early-flower stage, respectively) reduced the number of buds/flowerheads present at the end of the growing season 73% ($P < 0.01$; Table 1), and clipping in August (i.e., spotted knapweed plants in full-flower stage), June+July, or July+August reduced the number of buds/flowerheads 89% ($P < 0.01$) compared with no clipping. Clipping in June+August or June+July+August reduced the number of buds/flowerheads present at the end of the growing season 98% ($P < 0.01$) and clipping in July+August or June+July+August reduced number of buds/flowerheads 95% ($P < 0.01$) compared with no clipping.

Number of Seeds

Clipping in June reduced the number of doughy seeds 68% ($P < 0.01$; Table 2) compared with no clipping. Clipping in July or June+July reduced the number of doughy seeds 94% ($P < 0.01$), and clipping in August, June+July, June+August, July+August, or June+July+August reduced the number of doughy seeds 99% ($P < 0.01$) compared with no clipping. The number of intermediate seeds was reduced 82% ($P < 0.01$) when plants were clipped in June, reduced 96% ($P < 0.01$) when plants were clipped in July, June+July, or June+August, and reduced 99% ($P < 0.01$) when plants were clipped in

Table 1. Number of buds/flowerheads (±SE) produced per spotted knapweed plant in 2006 and 2007 after defoliation at different timings and combinations of timings on foothill rangeland in western Montana.

	Treatment							
Year	Control	June	July	August	June+ July	June+ August	July+ August	June+July +August
	(No. · plant^{-1})							
2006	23.8 (3.4)a[1]	7.8 (1.5)b	8.2 (2.1)b	2.6 (0.6)c	4.2 (2.2)c	0.3 (0.2)d	1.9 (0.9)cd	0.3 (0.2)d
2007	19.1 (3.4)a	4.0 (0.7)b	2.7 (1.0)bc	1.9 (0.6)cd	2.2 (1.2)ce	0.3 (0.2)de	1.4 (0.6)cd	0.4 (0.2)de
Mean	21.3 (2.4)a	5.9 (0.9)b	5.5 (1.3)b	2.3 (0.4)c	3.3 (1.3)c	0.3 (0.1)d	1.7 (0.5)ce	0.4 (0.1)de

[1]Means within rows followed by the same letter are not different ($P > 0.05$).

Table 2. Number of doughy, intermediate, and mature spotted knapweed seeds (±SE) per plant produced in 2006 and 2007 after defoliation at different timings and combinations of timings on foothill rangeland in western Montana.

		Treatment							
Seed Stage	Year	Control	June	July	August	June+ July	June+ August	July+ August	June+July +August
		---(No. · plant^{-1})---							
Doughy	2006	144.9 (30.4)a[1]	61.1 (16.9)b	13.5 (7.9)c	0c	16.0 (13.8)c	0c	0.3 (0.3)c	0c
	2007	155.5 (28.2)a	34.2 (9.6)b	6.6 (2.9)c	0c	1.6 (1.6)c	0c	1.2 (1.2)c	0c
	Mean	150.5 (20.1)a	47.7 (9.9)b	10.1 (4.2)c	0d	9.2 (7.3)cd	0d	0.8 (0.6)d	0d
Intermediate	2006	20.4 (3.5)a	6.9 (2.5)b	3.3 (2.4)bc	0c	1.3 (1.3)c	0c	0c	0c
	2007	29.0 (6.9)a	2.0 (0.5)b	1.3 (0.9)bc	0c	0.0 (0.0)c	0c	0c	0c
	Mean	24.9 (4.0)a	4.5 (1.4)b	2.3 (1.3)c	0d	0.7 (0.7)cd	0cd	0d	0d
Mature	2006	196.9 (35.1)a	22.6 (7.1)b	0.5 (0.5)c	0c	0.1 (0.1)c	0c	0c	0c
	2007	24.7 (6.3)a	4.5 (2.6)b	1.9 (0.9)bc	0c	0c	0c	0c	0c
	Mean	106.3 (26.1)	13.6 (4.2)	1.2 (0.5)	0	0.1 (0.1)	0	0	0
Total	2006	362.2 (61.8)a	90.6 (22.5)b	17.3 (9.8)c	0c	17.4 (15.2)c	0c	0.3 (0.3)c	0c
	2007	209.2 (37.5)a	40.7 (11.5)b	9.8 (4.4)c	0de	1.6 (1.6)cd	0de	1.2 (1.2)ce	0de
	Mean	281.7 (38.7)	65.7 (13.6)	13.6 (5.3)	0	9.9 (8.1)	0	0.8 (0.6)	0

[1]Means within rows followed by the same letter are not different (*P* > 0.05).

August, June+July, June+August, July+August, or June+July+August compared with no clipping.

The effect of clipping on the number of mature seeds varied between years (*P* < 0.01). Clipping in June 2006 reduced the number of mature seeds 89% (*P* < 0.01), and clipping at all other timings or combinations of timings in 2006 reduced the number of mature seeds 100% (*P* < 0.01) compared with no clipping. Clipping in June or July 2007 reduced the number of mature seeds 87% (*P* < 0.01), and clipping in July, August, June+July, June+August, July+August, or June+July+August 2007 reduced the number of mature seeds 99% (*P* < 0.01) compared with no clipping.

The effect of clipping on total number of seeds varied between years (*P* < 0.01). The total number of seeds was reduced 75% (*P* < 0.01) when plants were clipped in June 2006, and when plants were clipped at all other times or combinations of timings in 2006, the total number of seeds was reduced 98% (*P* < 0.01) compared with no clipping. Clipping in June 2007 reduced the total number of seeds 81% (*P* < 0.01). Total number of seeds was reduced 98% (*P* < 0.01) when plants were clipped in July, June+July, or July+August 2007, and clipping in August, June+July, June+August, or June+July+August 2007 reduced the total number of seeds 99.8% (*P* < 0.01) compared with no clipping. The total number of seeds was reduced 100% (*P* < 0.01) when plants were clipped in August, June+August, July+August, or June+July+August 2007 compared with no clipping.

Percent Viability of Seeds

No doughy seeds were viable throughout the study. Clipping in June reduced percent viability of intermediate seeds 57% (*P* < 0.01; Table 3), and clipping at all other timings or combinations of timings reduced percent viability of intermediate seeds 99% ($P < 0.01$) compared with no clipping. The effect of clipping on percent viability of mature seeds varied between years ($P < 0.01$). Percent viability of mature seeds was reduced 23% ($P < 0.01$) when plants were clipped in June 2006, and 99.6% ($P < 0.01$) when plants were clipped in July, August, June+July, June+August, July+August, or June+July+August 2006 compared with no clipping. Clipping in June or July 2007 reduced percent viability of mature seeds 58% ($P < 0.01$), and clipping at all other times or combinations of timings in 2007 reduced percent viability of mature seeds 100% ($P < 0.01$) compared with no clipping.

Number of Viable Seeds

The effect of clipping on the number of viable intermediate, mature, and total seeds varied between years ($P < 0.01$; Table 4). The number of viable intermediate seeds was reduced 77% ($P < 0.01$) when plants were clipped in June 2006, and the number of viable intermediate seeds was reduced 100% ($P < 0.01$) when plants were clipped at all other times or combinations of timings in 2006 compared with no clipping. Clipping at all timings or combinations of timings in 2007 reduced the number of viable intermediate seeds 99% ($P < 0.01$) compared with no clipping.

The number of viable mature seeds was reduced 88% ($P < 0.01$) when plants were clipped in June 2006 and 100% ($P < 0.01$) when plants were clipped at all other times or combinations of timings in 2006 compared with no clipping. Clipping in June or July 2007 reduced the number of viable mature seeds 87% ($P < 0.01$), and clipping in July, August, or any combination of timings in 2007 reduced the number of viable mature seeds 99% ($P < 0.01$) compared with no clipping.

Table 3. Viability (%) of intermediate and mature spotted knapweed seeds (±SE) per plant produced in 2006 and 2007 after defoliation at different timings and combinations of timings on foothill rangeland in western Montana.

Seed Stage	Year	Treatment							
		Control	June	July	August	June+ July	June+ August	July+ August	June+July +August
		(%)							
Intermediate	2006	25.0 (7.4)a[1]	13.5 (6.7)b	0c	0c	0c	0c	0c	0c
	2007	44.8 (7.4)a	16.7 (10.2)b	6.0 (6.0)bc	0c	0c	0c	0c	0c
	Mean	35.4 (5.6)a	15.1 (5.9)b	3.0 (3.0)c	0c	0c	0c	0c	0c
Mature	2006	89.0 (2.0)a	68.2 (12.0)b	2.0 (2.0)c	0c	0c	0c	0c	0c
	2007	89.0 (2.4)a	35.1 (14.6)b	40.0 (16.3)b	0c	0c	0c	0c	0c
	Mean	89.0 (1.5)	51.7 (10.0)	21.0 (9.1)	0	0	0	0	0

[1]Means within rows followed by the same letter are not different ($P > 0.05$).

Table 4. Number of viable intermediate and mature spotted knapweed seeds (±SE) produced per plant in 2006 and 2007 after defoliation at different timings and combinations of timings on foothill rangeland in western Montana.

		Treatment							
Seed Stage	Year	Control	June	July	August	June+ July	June+ August	July+ August	June+July +August
		(No. · plant^{-1})							
Intermediate	2006	6.1 (2.0)a[1]	1.4 (0.6)b	0c	0c	0c	0c	0c	0c
	2007	10.4 (2.4)a	0.3 (0.2)b	0.3 (0.3)b	0b	0b	0b	0b	0b
	Mean	8.4 (1.6)	0.9 (0.3)	0.2 (0.2)	0	0	0	0	0
Mature	2006	173.0 (30.3)a	20.1 (6.7)b	0.1 (0.1)c	0c	0c	0c	0c	0c
	2007	21.0 (4.9)a	3.5 (1.9)b	1.9 (0.9)bc	0c	0c	0c	0c	0c
	Mean	93.0 (22.8)	11.8 (3.9)	1.0 (0.5)	0	0	0	0	0
Total	2006	179.1 (29.8)a	21.5 (7.3)b	0.1 (0.1)c	0c	0c	0c	0c	0c
	2007	31.4 (5.7)a	3.8 (1.8)b	2.2 (1.2)bc	0c	0c	0c	0c	0c
	Mean	101.4 (22.3)	12.7 (4.2)	1.2 (0.6)	0	0	0	0	0

[1]Means within rows followed by the same letter are not different ($P > 0.05$).

The total number of viable seeds was reduced 88% ($P < 0.01$) when plants were clipped in June 2006 and 100% ($P < 0.01$) when clipped at all other times or combinations of timings in 2006 compared with no clipping. Clipping in June or July 2007 reduced the total number of viable seeds 91% ($P < 0.01$) and clipping in July, August, or any combination of timings in 2007 reduced the total number of viable seeds 99% ($P < 0.01$) compared with no clipping.

Discussion

New buds and flowers produced after plants were clipped at any time or combination of timings produced very few to no viable seeds. The number of buds/flowerheads, number of seeds, percent viability, and number of viable seeds was reduced both years, regardless of when plants were clipped.

Differences in plant responses between years may be attributed to variations in precipitation. In the Intermountain Region, the crop-year begins July 1 and ends June 30 of the following year. However, precipitation in July and August is typically very low and does not promote plant growth, therefore a crop-year beginning September 1 and ending June 30 may be more appropriate for assessing the influence of precipitation on rangeland plant productivity in this region (Sneva and Hyder 1962; Sneva and Britton 1983). Precipitation for the 2007 crop-year (beginning Sept. 1, 2006 and ending June 30, 2007) was 25 mm less than precipitation for the 2006 crop-year (beginning Sept. 1, 2005 and ending June 30, 2006) (WRCC 2007). The number of seeds produced by spotted knapweed is largely affected by precipitation during the growing season, with greater seed production during wet years (Schirman 1981; Sheley et al. 1998). The total number of seeds and viable seeds produced in my study was greater in 2006 than 2007, which I attribute to more precipitation during the 2006 crop-year.

My results demonstrated that clipping during the bolting stage or late-bud/early-flower stage reduced the number of buds/flowerheads 73%, while clipping during the full-flower stage reduced the number of buds/flowerheads 89% compared with unclipped plants. Similarly, when prescribed sheep grazing was applied in western Montana during the rosette stage or the late-bolting/early-bud stage, there was a 68% and 80% reduction, respectively, in the number of plants that flowered (Cox 1989). Fewer seedheads were also present at the end of the growing season in southeastern Idaho when prescribed sheep grazing was applied during the flowering stage than during the bolting stage (Launchbaugh and Hendrickson 2001).

The total number of seeds present at the end of the growing season was least when plants were clipped during the late-bud/early-flower stage, full-flower stage, or any combination of timings (with at least a 95% reduction). While clipping during the bolting stage reduced the total number of seeds produced compared with no clipping, clipping during the late-bud/early-flower or full-flower stages had a greater reduction in total seeds produced. Sheep grazing may reduce the rate of increase of spotted knapweed in native plant communities if the time of grazing is managed and spotted knapweed is grazed when grasses are going dormant (Olson et al. 1997). Sheep grazing spotted knapweed-infested communities may help re-establish a competitive balance between native grasses and spotted knapweed because knapweed may be most vulnerable to reduced seed production after rangeland grasses have set seed and knapweed forage volume and nutritive value is still high (Cox 1989; Olson and Wallander 2001; Thrift et al. 2008). In a moderate spotted knapweed infestation, sheep will consume less graminoids and more spotted knapweed when grazing occurs in the late-bud/early-flower stage rather than the bolting stage (Thrift et al. 2008).

How defoliation affects percent viability of spotted knapweed seeds has not been focused on in previous research. In my study, percent viability of intermediate seeds was reduced nearly 60% when plants were clipped during the bolting stage and almost 100% when plants were clipped at all other times or combinations of timings. Clipping during the late-bud/early-flower stage, full-flower stage, or any combination of timings in 2006 reduced percent viability of mature seeds nearly 100%. In 2007, percent viability of mature seeds was reduced 100% when plants were clipped during the full-flower stage or any combination of timings. The percent viability of mature seeds of unclipped plants for both years was 89% and intermediate seeds averaged 35% viability. The weighted average of mature and intermediate seed percent viability of unclipped plants for both years was 69%. This correlates to previous research findings of 60-82% viability of current years' seeds (Jacobs and Sheley 1998).

The objective of my study was to determine the appropriate timing of defoliation on spotted knapweed to reduce viable seed production. I found that clipping during the bolting stage reduced the number of viable seeds nearly 90% compared with no clipping and clipping during the late-bud/early-flower or full-flower stages or any combination of timings reduced the number of viable seeds almost 100% compared with no clipping. My results help explain why a previous study in southwestern Montana reported that more viable spotted knapweed seeds were recovered from seed bank soil cores from ungrazed areas than areas that were grazed by sheep in mid-June, July, and early

September (Olson et al. 1997). Spotted knapweed's prolific seed production and seed longevity make long-term control of spotted knapweed difficult and expensive. Jacobs and Sheley (1998) reported 998 to 7,815 viable seeds $\cdot$ m^{-2}. If defoliation via prescribed sheep grazing or mowing can result in a 90-100% reduction in viable seeds produced each year, successive years of defoliation will significantly reduce contributions to the seedbank, fewer seedlings will become established, fewer adult plants will produce viable seeds, and, hopefully, over time the spotted knapweed population will be reduced.

Previous research has shown that sheep consume the buds and flowerheads of spotted knapweed, including in late summer (Olson and Wallander 2001), and prescribed sheep grazing can be used to reduce seed production (Olson et al. 1997). My results indicate that the most effective time of defoliation is during the late-bud/early-flower or full-flower stage, with nearly a 100% reduction in viable seed production. However, 22% of mature spotted knapweed seeds remain viable after passing through the digestive system of a sheep (Wallander et al. 1995). Because mature spotted knapweed seeds are not formed until post-flowering in mid-August (Watson and Renney 1974), and if grazing sheep ingest spotted knapweed buds and flowerheads before the full-flower stage, seed production and viability should be reduced and the seeds that the sheep are consuming will not be viable either. Also, any seeds that the sheep may collect in their wool will not be viable.

Management Implications

Spotted knapweed reproduces largely by seed, therefore, prescribed sheep grazing or mowing should effectively suppress reproduction of spotted knapweed when plants are defoliated during the bolting, late-bud/early-flower or full-flower stages. New flowers that are produced in the same season following defoliation produce very few to no viable seeds. Defoliation during the bolting stage reduced the number of viable seeds nearly 90%. Defoliation during the late-bud/early-flower stage, full-flower stage, or any combination of timings reduced the number of viable seeds nearly 100%. If spotted knapweed is grazed or mowed during the bolting stage, an additional defoliation during the late-bud/early-flower or full-flower stage is recommended for the best control. If plants are grazed or mowed during the late-bud/early-flower or full-flower stage, an additional defoliation is not necessary. If sheep graze spotted knapweed during the bolting or late-bud/early-flower stage, sheep do not need to be quarantined because the plants do not contain viable seed. If sheep graze during the full-flower stage, sheep will likely ingest viable spotted knapweed seeds and should be quarantined in a corral for seven days to allow viable seeds to be excreted (Wallander et al. 1995). If sheep graze during the bolting or late-bud/early-flower stage and again during the full-flower stage, sheep do not need to be quarantined because the spotted knapweed plants do not contain viable seeds. If spotted knapweed is mowed during the full-flower stage, the danger exists that viable seeds are present and will be contributed to the soil.

Literature Cited

Arnold, G. W., and M. L. Dudzinski. 1978. Ethology of free ranging domestic animals. New York, NY: Elsevier Scientific Publishing. 198 p.

Carpinelli, M. 2005. *Plant conservation alliance's alien plant working group. Available at:* http://www.nps.gov/plants/alien/. *Accessed 6 October 2007.*

Cox, J. W. 1989. Observations, experiments and suggestions for research on the sheep-spotted knapweed relationship. *In*: P. K. Fay and J. R. Lacey [EDS.], Proceedings of the Knapweed Symposium. 4-5 April 1989; Bozeman, MT: Montana State University, Plant and Soil Science Department. p. 79-82.

Davis, E. S. 1990. Spotted knapweed (*Centaurea maculosa* L.) seed longevity, chemical control and seed morphology [thesis]. Bozeman, MT: Montana State University. 109 p.

Davis, E. S., P. K. Fay, T. K. Chicoine, and C. A. Lacey. 1993. Persistence of spotted knapweed (*Centaurea maculosa*) seed in soil. *Weed Science* 41:57-61.

DiTomaso, J. M. 2000. Invasive weeds in rangelands: species, impacts, and management. *Weed Science* 48:255-265.

Grabe, D. F. 1970. Tetrazolium testing handbook for agricultural seeds. Contribution No. 29 of the Handbook on Seed Testing. Association of Offical Seed Analysts. 62 p.

Griffith, D., and J. R. Lacey. 1991. Economic evaluation of spotted knapweed (*Centaurea maculosa*) control using picloram. *Journal of Range Management* 44: 43-47.

Hanley, T. A. 1982. The nutritional basis for food selection by ungulates. *Journal of Range Management* 35:146-151.

Harris, P., and R. Cranston. 1979. An economic evaluation of control methods for diffuse and spotted knapweed in western Canada. *Canadian Journal of Plant Science* 59:375-382.

Hirsch, S. A., and J. A. Leitch. 1996. The impact of knapweed on Montana's economy. Fargo, ND: North Dakota State University Agricultural Experiment Station, Agricultural Economics Report 355. 43 p.

Jacobs, J. S., and R. L. Sheley. 1998. Observation: life history of spotted knapweed. *Journal of Range Management* 51:665-673.

Kuehl, R. O. 2000. Design of experiments: statistical principles of research design and analysis, 2nd Edition. Pacific Grove, CA: Duxberry Press. 666 p.

Lacey, C. A., J. R. Lacey, T. K. Chicoine, P. K. Fay, and R. A. French. 1986. Controlling knapweed on Montana rangeland. Bozeman, MT: Montana State University Extension Service Circular 311. 15 p.

Lacey, J. R. 1983. A complete takeover by knapweed in 2001? *Montana Farmer-Stockman* 70:32-34.

Lacey, J. R., C. B. Marlow, and J. R. Lane. 1989. Influence of spotted knapweed (*Centaurea maculosa*) on surface runoff and sediment yield. *Weed Technology* 3:627-631.

Launchbaugh, K., and J. Hendrickson. 2001. Prescription grazing for *Centaurea* control on rangelands. *In:* L. Smith [ED.]. The First International Knapweed Symposium of the Twenty-First Century. 15-16 March 2001; Coeur d' Alene, ID: USDA, Agricultural Research Service. p. 27-32.

Mueggler, W.F., and W.L. Stewart. 1980. Grassland and shrubland habitat types of western Montana. General Technical Report INT-66., Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 154 p.

Nolan, D. G., and M. K. Upadhyaya. 1988. Primary seed dormancy in diffuse and spotted knapweed. *Canadian Journal of Plant Science* 68:775-783.

Olson, B. E., and J. R. Lacey. 1994. Sheep: a method for controlling rangeland weeds. *Sheep & Goat Research Journal* 10:105-112.

Olson, B. E., R. T. Wallander, and J. R. Lacey. 1997. Effects of sheep grazing on a spotted knapweed-infested Idaho fescue community. *Journal of Range Management* 50:386-390.

Olson, B. E., and R. T. Wallander. 2001. Sheep grazing spotted knapweed and Idaho fescue. *Journal of Range Management* 54:25-30.

Rinella, M. J., J. S. Jacobs, R. L. Sheley, and J. J. Borkowski. 2001. Spotted knapweed response to season and frequency of mowing. *Journal of Range Management* 54:52-56.

SAS Institute. 2004. SAS/STAT 9.1 User's Guide. Cary, NC: SAS Institute, Inc. 5136 p.

Schirman, R. 1981. Seed production and spring seedling establishment of diffuse and spotted knapweed. *Journal of Range Management* 34:45-47.

Sheley, R. L., J. S. Jacobs, and M. F. Carpinelli. 1998. Distribution, biology, and management of diffuse (*Centaurea diffusa*) and spotted knapweed (*Centaurea maculosa*). *Weed Technology* 12:353-362.

Sneva, F. A., and D. N. Hyder. 1962. Estimating herbage production on semiarid ranges in the Intermountain Region. *Journal of Range Management* 15:88-93.

Sneva, F., and C. M. Britton. 1983. Adjusting and forecasting herbage yields in the Intermountain big sagebrush region of the steppe province. Corvallis, OR: Oregon State University Agricultural Experiment Station Bulletin 659. 61 p.

Steel, R. G. D., and J. H. Torrie. 1980. Principles and procedures of statistics: a biometrical approach, 2nd Edition. New York, NY: McGraw-Hill. 633 p.

Thompson, M. J. 1996. Winter foraging response of elk to spotted knapweed removal. *Northwest Science* 70:10-19.

Thrift, B. D. 2005. Summer diets of sheep grazing spotted knapweed-infested foothill rangeland in western Montana [thesis]. Bozeman, MT: Montana State University. 59 p.

Thrift, B. D., J. C. Mosley, T. K. Brewer, B. C. Roeder, B. E. Olson, and R. W. Kott. 2008. Prescribed sheep grazing to suppress spotted knapweed on foothill rangeland. *Rangeland Ecology and Management* 61:18-25.

Tyser, R. W., and C. H. Key. 1988. Spotted knapweed in natural area fescue grasslands: an ecological assessment. *Northwest Science* 62:151-160.

USDA, NRCS. 2007a. *The PLANTS database. Available at:* http://plants.usda.gov. *Accessed 6 October 2007.*

USDA, NRCS. 2007b. *Web soil survey of Powell County area, MT. Available at:* http://websoilsurvey.nrcs.usda.gov/app/. *Accessed 6 November 2007.*

Wallander, R. T., B. E. Olson, and J. R. Lacey. 1995. Spotted knapweed seed viability after passing through sheep and mule deer. *Journal of Range Management* 48:145-149.

Watson, A. K., and A. J. Renney. 1974. The biology of Canadian weeds. *Centaurea diffusa* and *C. maculosa*. *Canadian Journal of Plant Science* 54:687-701.

[WRCC] Western Regional Climate Center. 2007. *Period of record monthly climate summary, Ovando 9 SSE, Montana (246304). Available at:* http://www.wrcc.dri.edu. *Accessed 6 November 2007.*